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Abstract: Evolutionary conflicts of interest arise whenever genetically different individuals interact and their routes to fitness maximization differ. Sexual selection favors traits that increase an individual's competitiveness to acquire mates and fertilizations. Sexual conflict occurs if an individual of sex A's relative fitness would increase if it had a "tool" that could alter what an individual of sex B does (including the parental genes transferred), at a cost to B's fitness. This definition clarifies several issues: Conflict is very common and, although it extends outside traits under sexual selection, sexual selection is a ready source of sexual conflict. Sexual conflict and sexual selection should not be presented as alternative explanations for trait evolution. Conflict is closely linked to the concept of a lag load, which is context-dependent and sex-specific. This makes it possible to ask if one sex can "win." We expect higher population fitness if females win.

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The Relationship between Sexual Selection and Sexual Conflict

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Evolutionary conflicts of interest arise whenever genetically different individuals interact and their routes to fitness maximization differ. Sexual selection favors traits that increase an individual's competitiveness to acquire mates and fertilizations. Sexual conflict occurs if an individual of sex A's relative fitness would increase if it had a "tool" that could alter what an individual of sex B does (including the parental genes transferred), at a cost to B's fitness. This definition clarifies several issues: Conflict is very common and, although it extends outside traits under sexual selection, sexual selection is a ready source of sexual conflict. Sexual conflict and sexual selection should not be presented as alternative explanations for trait evolution. Conflict is closely linked to the concept of a lag load, which is context-dependent and sex-specific. This makes it possible to ask if one sex can "win." We expect higher population fitness if females win.

Many published studies ask if sexual selection or sexual conflict drives the evolution of key reproductive traits (e.g., mate choice). Here we argue that this is an inappropriate question. By analogy, G. Evelyn Hutchinson (1965) coined the phrase "the ecological theatre and the evolutionary play" to capture how factors that influence the birth, death, and reproduction of individuals (studied by ecologists) determine which individuals reproduce, and "sets the stage" for the selective forces that drive evolutionary trajectories (studied by evolutionary biologists). The more modern concept of "eco-evolutionary feedback" (Schoener 2011) emphasizes that selection changes the character of the actors over time, altering their ecological interactions. No one would sensibly ask whether one or the other shapes the natural world, when obviously both interact to determine the outcome.

So why have sexual conflict and sexual selection sometimes been elevated to alternate explanations? This approach is often associated with an assumption that sexual conflict affects traits under direct selection, favoring traits that alter the likelihood of a potential mate agreeing or refusing to mate because it affects the bearer's immediate reproductive output, whereas "traditional" sexual selection is assumed to favor traits that are under indirect selection because they increase offspring fitness. These "traditional" models are sometimes described as "mutualistic" (e.g., Pizzari and Snook 2003; Rice et al. 2006), although this term appears to be used

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only when contrasting them with sexual conflict models. The investigators of the original models never describe them as "mutualistic," which is hardly surprising given that some males are rejected by females.

In this review, we first define sexual conflict and sexual selection. We then describe how the notion of a "lag load" can reveal which sex currently has greater "power" in a sexual conflict over a specific resource. Next, we discuss why sexual conflict and sexual selection are sometimes implicitly (or explicitly) presented as alternative explanations for sexual traits (usually female mate choice/resistance). To illustrate the problems with the assumptions made to take this stance, we present a "toy model" of snake mating behavior based on a study by Shine et al. (2005). We show that empirical predictions about the mating behavior that will be observed if females seek to minimize direct cost of mating or to obtain indirect genetic benefits were overly simplistic. This allows us to make the wider point that whom a female is willing to mate with and how often she mates are often related questions. Finally, we discuss the effect of sexual conflict on population fitness.

DEFINING SEXUAL SELECTION AND SEXUAL CONFLICT

With the exception of artificial experimental breeding designs (see below), sexual conflict is likely to be present whenever there is sexual reproduction. This is true regardless of whether there is anisogamy with males and females or isogamy with two or more mating types (Matsuda and Abrams 1999). We therefore argue that little is gained by asking how sexual selection will differ in the presence and in the absence of sexual conflict. It makes more sense to ask what kinds of traits are favored in each sex, and why, given the inevitable existence of sexual conflict over at least some aspects of reproduction. Our argument relies on the fact that once sexual conflict and sexual selection are appropriately defined, it is near impossible to envisage a biologically plausible situation in which sexual selection exists without sexual conflict, or vice versa.

There are many definitions of sexual selection, extending Darwin's original proposal that sexual selection "depends on the advantage that certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (Darwin 1871, p. 256). One widely accepted definition is that "sexual selection is the differences in reproduction that arise from variation among individuals in traits that affect success in competition over mates and fertilizations" (Andersson 1994, p. 31). There can be practical difficulties in applying this definition to identify sexually selected traits. For example, is a male stickleback that builds a nest selected to do so because it improves offspring survival (natural selection) or because he needs a nest to attract mates? Such "gray zones" aside, sexual selection is a straightforward notion.

Sexual conflict has been defined in many subtly different ways, but these definitions all rely on the fact that evolutionary conflicts of interest can arise whenever two genetically different individuals ("actors") interact (Dawkins 1976; Dawkins and Krebs 1979; Parker 1979). Sexual conflict is comparable to parent–offspring conflict (Parker 2006). In both cases there are shared interests between the two actors (parents "want" their offspring to succeed; males and females "want" to breed), but this does not preclude disagreements over how this common goal is achieved.

Sexual conflict can occur over every facet of breeding. It starts with who will mate search (Hammerstein and Parker 1987), proceeds to whether to reject or accept a potential mate (Parker 1979), and then encompasses how mating and gamete transfer occur. After mating, there might be conflict over whether or not additional matings with other individuals are favored (Baer et al. 2001; Fromhage 2012). Finally, there is conflict over how many offspring are produced, when they are produced, and how much each parent invests into these offspring (e.g., disputes over parental care [Lessells 2006]). Sexual conflict extends beyond traits under sexual selection in one sex and responses by the other sex to their effects on its fitness. It is a much broader concept.

Despite consensus that sexual conflict arises because of genetic differences between potential mates, its definitions are a confusing mixture of statements about costs imposed on a single individual during a mating encounter, differences in mean fitness between the sexes (or temporal changes in mean fitness), or lowered population fitness. To avoid some easy pitfalls, and to make conceptual points, we propose an unorthodox definition that is, hopefully, thought-provoking.

There is sexual conflict if a hypothetical cost-free "tool" allowed some individuals of sex A to alter what individuals of sex B do at a cost to B, such that sex A individuals with the "tool" are then selectively favored over those without it.

The noun "tool" and the verb "to do" should be interpreted broadly. Most obviously, individuals of sex B could change their behavior or morphology when interacting with A individuals who have the tool. For example, instead of B incessantly attempting to mate with A, it now leaves A in peace; or B no longer includes chemicals in its ejaculate that reduce A's lifespan. Our definition is therefore readily applied to interlocus sexual conflict. It can also be applied to intralocus sexual conflict (i.e., genes that elevate fitness in an individual of sex B but reduce it in one of sex A [van Doorn 2009; also see work by Haig et al. 2014]). Here, the tool would be one that allowed an individual of sex A to alter its genes (or their expression) so that individuals with the tool are selectively favored over those without it, but these genetic modifications then impose a cost when expressed in an individual of sex B.

We are not assuming that the tool exists. Sexual conflict only requires that the current situation is suboptimal relative to a hypothetical alternative. It is the potential for selection should such a tool arise. It should also be noted that we could imagine scenarios in which several potential tools could improve fitness. It is then sufficient that one of them satisfies the definition for there to be conflict. For example, sex-specific gene expression might be a tool that benefits both sexes. This does not satisfy the part of the definition in which we require that tool use is costly to the other sex. Do we then erroneously conclude that sexual conflict is absent when sex-specific expression has not yet evolved but would be selected for if it arose? No, because the potential for sex-specific expression to resolve a conflict does not prevent another tool from existing (e.g., alleles that simply lead to the optimal female phenotype at the expense of male fitness). Our definition as a whole resembles that of Hosken et al. (2009) who asked what would happen if one sex had complete control of trait expression in the other sex.

We have specified that possession of the hypothetical tool is cost-free because the presence of costs might be the very factor preventing an individual from reducing sexual conflict (from its perspective). This, of course, would not mean that sexual conflict had vanished. For example, resisting mating attempts might be so costly for a female turtle that her best option is to acquiesce (convenience polyandry [Lee and Hays 2004]). If she could do something to prevent males from mating, however, and this was cost-free, then the actual behaviors of males—that is, how often they actually mated with her—would change. If additional matings were costly for females, then females with the cost-free tool would be favored by selection. This thought experiment reveals that an underlying sexual conflict exists despite females showing no overt resistance to male mating attempts.

In reality, evolutionary innovations can equip individuals with "tools" that, although rarely cost-free, are still selected for in situations with sexual conflict. It is reasonable to assume that the resultant changes will reduce the relative fitness of the affected sex B individuals. If these changes were beneficial for both A and B, they are likely to have already arisen. Sexual conflict therefore generates sexually antagonistic selection (Lessells 2006; van Doorn 2009).

Our definition emphasizes changes in relative fitness within a single sex in a single generation. This avoids the complications that ensure when trying to interpret statements such as "evolutionary changes in male behavior impose costs on females" or "on absolute fitness," given that female fitness might remain unchanged when measured in a population at demographic equilibrium (see Frank and Slatkin 1992; Frank

2012). For example, if female lifetime fecundity declines from one generation to the next because of male-imposed costs, density-dependent juvenile survival might compensate so that each female still recruits on average one daughter to form the next generation (the life history stage of compensatory density-dependent mechanisms need not be the juvenile stage, but if no equivalent mechanisms were in place, populations would generally not persist). Also, we avoid making statements that inappropriately contrast the effect of sexual conflict on the mean fitness of each sex (e.g., Pizzari and Snook 2003; see Arnqvist 2004). In diploid species each offspring has a mother and father so the total number of offspring sired by males cannot differ from the number produced by females ("Fisher condition" [Houston and McNamara 2005]).

LAG LOADS AND WHAT WE CAN LEARN FROM THEM

Our definition captures the idea that sexual conflict involves each sex imposing a "lag load" on the other sex (Rice et al. 2006). The concept of a lag load was used by Maynard Smith (1976) to describe cases in which the average trait value in a population is below its optimum because the selective environment deviates from an earlier state. For sexual conflict, this can be envisaged as the fitness improvement that a sex A individual could achieve over same-sex competitors if it made sex B individuals act to maximize A's reproductive value. This is the deviation of the current environment from an earlier, hypothetical best-case scenario for A.

Sexual conflict is a broad concept, so our definition is intentionally imprecise about the exact nature of the lag load. For example, if A is male and B is female, is "she will mate with you" the scenario for which lag load is measured, or is it "she will mate with you and then never mate again with anyone else"? Lag loads are context-dependent, and realizing this highlights why sexual conflict is so ubiquitous. For example, consider a peahen that is freely able to choose the best peacock with whom to mate. There is still a lag load for her regarding parenting. A mutant female with the power to turn peacocks into ostrich-like males who care for her chicks could benefit by more rapidly producing an additional egg clutch.

Even if we momentarily ignore conflicts over parental care, sexual conflict is still present in even the most "traditional" sexual selection scenario of displaying males and choosy females. Why? A male who is never rejected by females will have greater fitness. This does not happen because choosy females reject many males. Sexual conflict is therefore ongoing. It is even more instructive to recognize the difference between a signaling system that makes it easiest for females to rank males and one that evolves because males try to outcompete each other (van Doorn and Weissing 2006). The fact that no matings occur in the "conflict zone" (*sensu* Parker 1979, 2006), in which only one of the two individuals benefits from a mating, does not make the system fully mutualistic. Male–male competition introduces inefficiencies into mate assessment that are detrimental to females.

Who Has Power?

This leads us to another topic: power, and whether it is possible for one sex to be on the winning side of sexual conflict. If we focus on conflicts over whether mating occurs after encountering a potential mate, it is useful to ask whether one sex currently "controls" or has "power" in this zone of conflict. Consider an example with major fitness consequences: There is a zone of conflict over the values of inbreeding depression that can make sibling mating beneficial for each sex. For a male who suffers no opportunity cost to mating, it is adaptive to mate with his sister up to an inbreeding depression δ value as high as $2/3$. For a female, who cannot have the same egg fertilized by another (unrelated) male if her brother fertilizes it, the threshold is lower at $\delta = 1/3$ (Parker 1979, 2006).

The lag load for females is clearly lower if they have the power to decide whether mating with a sibling occurs (in which case there is no female lag load) than if males can overcome their sisters' resistance to mating when $1/3 < \delta < 2/3$. In this sense, statements that it is

meaningless to ask which sex "wins" during a specific sexual conflict are overly strong (e.g., Arnqvist 2004). Sex A "has its own way" more than sex B if there are no conceivable ways in which B could behave better for the fitness of an individual of sex A in the context of the specified conflict. In this sense, A is the winner. This makes it valid to ask, although not necessarily easy to answer, questions such as whether certain adaptive traits, such as flight, have shifted sexual power toward females in birds when compared to the situation in less mobile mammals in which females cannot escape harassment as readily (Pradhan and van Schaik 2009). This might have consequences for the relative prevalence of ornaments versus armaments, if these trait types have different effects on female fitness.

The comparisons necessary to make statements about lag loads force us to deal with hypothetical scenarios. Pragmatically speaking, sensible questions about lag load are constrained by what occurs naturally or can be experimentally mimicked. The latter can involve clever experiments. For example, Rice et al. (2006) investigated male lag load when already mated females resist male courting effort. Males provided with a limitless supply of virgin females had a sevenfold potential reproductive output compared with a more natural setting that takes into account nonvirgin females' reluctance to remate (Rice et al. 2006). This difference can be interpreted as a measure of the male lag load—namely, the increase in reproductive success if he could find a cost-free way to ensure that every mated female encountered would mate with him (leaving aside issues about the share of paternity).

Removing Sexual Conflict Also Removes Sexual Selection

In nature, it is very rare to find monogamous pairs that form randomly, mate for life, and never remate if widowed (Hosken et al. 2009). Nevertheless, this hypothetical scenario provides a useful benchmark because it favors traits that remove sexual conflict and is experimentally tractable (see the review by Edward et al. 2010). The evolutionary interests of every interacting male and female (i.e., each pair) become identical, and selection acts to maximize their joint lifetime reproductive output. One can then quantify by how much lifetime reproductive success increases when wild-type individuals encounter opposite sex individuals from the experimental rather than their own population. The greater the increase in reproductive output, the larger the lag load due to sexual conflict.

Monogamous experimental populations, with random assignment of mates, are equally well described as ones in which sexual selection has been removed. The equivalency between sexual selection and conflict in this setting is unsurprising. Whenever sexual selection occurs, we can always conceive of ways in which, for example, a female would benefit if her mate invested less into trying to acquire other females or gain paternity assurance and more into her own survival or fecundity. To remove sexual conflict, it is therefore necessary to remove sexual selection.

Eliminating sexual selection, in contrast, does not always remove sexual conflict, because the conflict extends beyond mating and gaining access to opposite sex gametes to, for example, parental investment decisions. Nonetheless, sexual selection is clearly the most important source of sexual conflict. To see that it is more ubiquitous than, for example, conflicts over care, one only has to recall that neither sex offers parental care in most animal species (and offspring therefore do not "expect" to receive it).

The pervasiveness of sexual selection and the associated sexual conflict (and its context specificity) is well illustrated by considering a seemingly highly cooperative scenario in which the sexes always agree to mate when they meet: finding mates in a low-density population in which both sexes' reproductive rates are limited by mate encounters. There is no conflict over mating per se. Strong sexual selection on mate-location ability, likewise, seems mutually beneficial because individuals of neither sex can be certain that they will encounter mates at a sufficiently high rate. The Bateman gradient, a measure of whether selection favors an increase in the mating rate, is positive for both sexes

when it is mainly measured between zero or one mate (Kokko et al. 2012).

Even so, sexual conflict persists. The problem is precisely analogous to parental care, in which individuals of sex A benefit if sex B cares more. This allows sex A to reduce care and invest in other, more self-serving, fitness components. If increased mate searching is energetically costly or dangerous, or if signals that reveal an individual's location are costly, then a female would benefit if males "worked harder" to find her and vice versa. Clearly, one of these activities must happen, or individuals will not find each other. Models indeed show that if one sex searches more efficiently, the other sex then adaptively reduces its own search effort (Hammerstein and Parker 1987; Kokko and Wong 2007).

ONCE WE REALIZE THERE IS ALWAYS SEXUAL CONFLICT, WHAT HAPPENS TO GENETIC BENEFITS?

There are three main types of traits favored by sexual selection because they increase access to mates. Traits can (a) make it easier to locate mates (e.g., locomotor efficiency, olfactory powers); (b) confer an advantage during direct physical contests between rivals (i.e., weapons); and (c) increase attractiveness to the opposite sex (e.g., ornaments). These categories appear to differ in the extent to which we need to consider the coevolution of the two sexes. Specifically, traits that increase attractiveness are associated with mate choice and mating preferences in the opposite sex. This can generate genetic correlations between ornaments, preferences, and other components of fitness (i.e., viability) (Kokko et al. 2006). Much of the debate about the relationship between sexual conflict and sexual selection over the last decade has been about mate choice. For brevity, we follow convention and describe cases in which females choose males.

Given sexual conflict, it is easy to see that females might increase their relative fitness by being choosier (i.e., choosiness is a "tool"). For example, females could prefer males that offer more nutritious nuptial gifts (Lewis and South 2012) or are less likely to inflict damage while mating (if this can be assessed before copulating). It is uncontroversial that sexual conflict can promote the evolution of mating preferences that involve a female actively sampling males and choosing those that confer greater direct benefits or, phrased differently, impose smaller costs. Both yield a direct benefit because choice elevates a female's lifetime fecundity. Here, we can explain the evolution of female behavior without considering genetic (indirect) benefits. Adaptive mate choice need not elevate offspring fitness because of the genes they inherit.

Slightly differently, it has been argued that female choice (which includes behavioral resistance to mating because this affects which types of males become mates) is favored not because it increases the likelihood that certain types of males mate, but rather because it lowers a female's mating rate (i.e., choosiness reduces the number of potential mates; Gavrilets et al. 2001). The evolution of choice is then seen to be the result of selection due to sexual conflict over mating. Conflict occurs because males usually gain fitness from each successive mating (males almost always have a positive Bateman gradient), whereas females that mate multiply show little gain, and usually a decline, in fitness after a certain number of matings (e.g., Arnqvist et al. 2004). This decline can reflect time and predation costs or is itself the product of sexual conflict that favors males with traits that increase their share of paternity and/or the female's rate of offspring production but, in so doing, damage females (Morrow et al. 2003). Again, it is argued that choosiness is selected for because of direct benefits that arise because of sexual conflict, not genetic benefits (Gavrilets et al. 2001).

There is much debate as to whether sexual conflict over mating rates or benefits of mating with specific males best explain the evolution of female mating behavior (for empirical examples, see Friberg and Arnqvist 2003; Forstmeier 2004; Shine et al. 2005). We believe this dichotomy is an unhelpful way to frame the question. The real issue is more nuanced, and it was extensively discussed before the explosion of interest in sexual conflict in the early 2000s (e.g., Kirkpatrick and Barton 1997). How much do

genetic and direct benefits respectively contribute to selection that maintains costly mating preferences?

It is crucial to recognize that preference or resistance traits (for their different connotations, see Gavrilets et al. 2001) that affect the likely identity of the average mate will usually also change the number of mates per breeding cycle. For example, if a female has a strong preference for unusually large males, the rarity of such males in the population will automatically reduce her mating rate if she follows a rule of only mating with those males that exceed a size threshold (Kokko and Mappes 2013). Mate number and identity can be decoupled if females show strict monandry, but this is extremely rare (Jennions and Petrie 2000). Completely indiscriminate mating can also, in principle, eliminate this relationship, but in reality it often leads to indirect mate choice *sensu* Wiley and Poston (1996). If, for example, females arriving on a lek mated with all the males present (an unlikely scenario) or, alternatively, with just one randomly chosen male, their behavior would cause strong selection for males with stamina. Indeed, lek attendance is a strong correlate of male mating success (Hill 1991; Focardi and Tinelli 1996; Rintamäki et al. 2001; Friedl and Klump 2005). Mating truly randomly can be surprisingly difficult.

It is understandable why the correlation between mate identity and mating rate is easily forgotten: The history of the field encourages us to ignore it. The literature is largely split into "sexual conflict models" that emphasize selection for an optimal mating rate (e.g., Gavrilets et al. 2001; Rowe et al. 2005; Hoyle and Gilburn 2010; Kazancioglu and Alonzo 2012) and "mate choice models" that emphasize the identity of mates and the associated gains (direct or genetic), but do not explicitly address the number of mates or matings (for reviews, see Kokko et al. 2006; Kuijper et al. 2012). Consequently, tests of "sexual conflict models" as the driver of female mating behavior tend to consider the perceived alternative (i.e., the behavior predicted by mate choice models) in overly simplistic terms. Reality is more complex. For example, Rice et al. (2006) describe a fascinating set of experiments in *Drosophila* that removed the possibility of "trading up" on an earlier mating by preventing females from remating. Females mating less often is then equated with the absence of genetic benefits. In many cases, however, mating less often is indicative of stronger, not weaker, choosiness (Kokko and Mappes 2013; see also the debate on resistance as choice in Cordero and Eberhard [2003] and Rowe et al. [2005]). In general, it is challenging to predict what type of female behavior indicates increased choosiness. To highlight the complexity of the issue, we draw inspiration from a representative study on garter snakes (*Thamnophis sirtalis*) by Shine et al. (2005).

How to Be Choosy in a World of Coercive Mating

Garter snakes overwinter in communal dens. In summer, females rapidly disperse from the den, where male density is very high, to outlying areas with fewer males. Dispersal is a form of evasive, resistance-like behavior that reduces encounters with males that attempt to forcibly mate. Shine et al. (2005) asked whether female evasion acts to minimize cost imposed by male sexual harassment (labeled "sexual conflict") or is a form of indirect mate choice that generates a selective filter favoring certain males (labeled "traditional or mutualistic sexual selection," and even described as "cooperative" by the investigators). They explicitly equate choosiness with less effort spent evading males: "The hypothesis of indirect mate choice generates specific predictions... females will tolerate prolonged courtship rather than attempt to evade their suitors (because prolonged courtship would allow the female to assess male phenotype and thus select an appropriate mate)." We present a toy mathematical model inspired by mating in garter snakes to show that predicting female behavior from the mate choice hypothesis is more difficult than it first appears.

To investigate a hypothesis about indirect mate choice, we need to specify how female behavior affects the distribution of both mate number and identity. To allow for a conceptually simple possibility of indirect genetic bene-

fits, we assume two types of males: those that are either efficient or inefficient at harassing females into mating when other males also compete for females. Producing efficient harassers will elevate a sons' mating success, regardless of whether or not other females "prefer" to be harassed. This creates the potential for genetic benefits of nonrandom mating. Let the proportion of efficient harassers be q and that of inefficient harassers $1 - q$.

Females move away from the den area at speed s. To provide a minimal model, we ignore any cost to moving faster, although the model could be easily modified such that reaching a large s is only possible if the female possesses physiological adaptations that impose costs on other life history components. In the den area, the number of males that successfully harass a female into mating is a declining function of s: Faster females leave the area sooner. The function is weighted so that efficient harassers obtain more matings when females move at a given speed, and the performance difference between efficient and inefficient harassers is more pronounced for faster females. Our examples are derived assuming that the number of efficient harassers that achieve a mating with the female is $q5e^{-s}$, whereas the number of inefficient harassers doing so is $(1 - q)4e^{-1.2s}$ (Fig. 1). These are the means of a Poisson distribution of mate numbers. So, for example, if all males are good harassers and a female moves very slowly ($s \approx 0$), she will, on average, mate five times before leaving the den area if all males are efficient harassers or four times if all males are inefficient.

We assume that female reproductive success (direct fitness) is maximized if she mates exactly once in the den area ($w_1 = 1$) and is lower if she mates more often: generally $w_n = e^{-k(n-1)}$, in which $n \geq 1$ is the number of matings and k is a parameter. A mathematical prediction also borne out by data (Shine et al. 2005) is that a fast female might not mate in the den area. Little is known about the fitness consequences of this, so we vary it using the factor w_0 (here 0 refers to zero matings in the den). It is clearly possible for a female to mate outside the den; efficient harassers might still outperform inefficient ones here, but for simplicity we assume their performance is now equally efficient, so the probabilities that a female mates with each type of male is q and $1 - q$, respectively, when outside the den. If finding a male outside the den requires effort, or if matings there are relatively more costly, then $w_0 < 1$. There are two questions:

1. To maximize direct benefits, how fast should a female move given the negative effect of the number of mates on fitness (this favors higher speeds) and a decline in fitness outside the den area (i.e., $w_0 < 1$; this favors lower speeds)?
2. What speed maximizes genetic benefits?

We assume $w_0 < 1$ to be able to provide a thought-provoking answer to these questions, and we leave it to the reader to visualize why the same set of results would apply for $w_0 > 1$ if we also introduce physiological costs that prevent a female from moving infinitely fast.

The answer to (1) is relatively straightforward (Fig. 2A,B). For (2), there are modeling

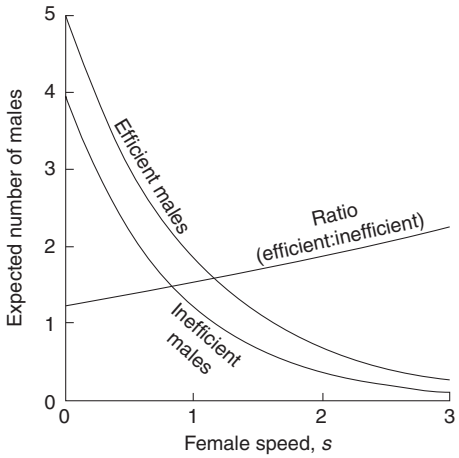

Figure 1. The assumptions of the toy model. The relationship between female speed, s, and the expected number of efficient harassers that mate with her (upper declining curve) and inefficient harassers (lower declining curve), each plotted for the scenario in which this male type predominates in the population. The increasing curve shows that the proportion of eggs fertilized by the former increases with s, here plotted assuming that both types are equally common ($q = 0.5$).

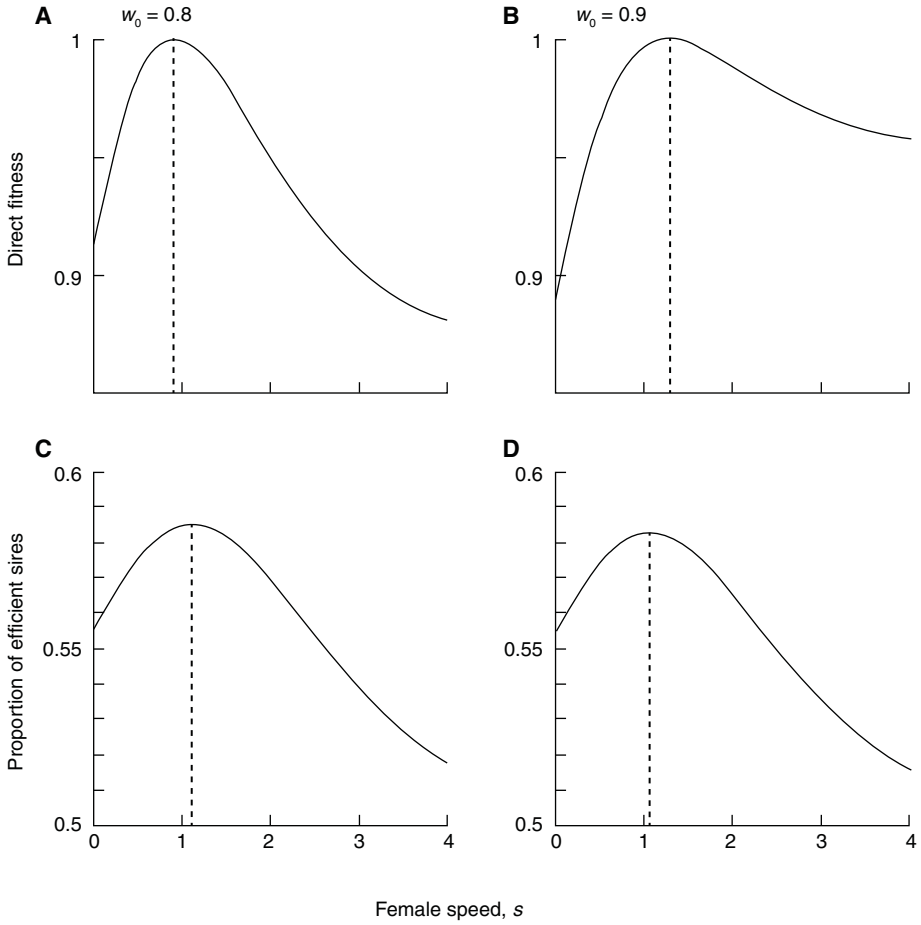

Figure 2. Two scenarios (*A*,*C*) $w_0 = 0.8$ and (*B*,*D*) $w_0 = 0.9$, where we plot (*A*,*B*) the consequent direct fitness, measured as

$$w_0\, e^{-\lambda} + \sum_{n=1}^{\infty} e^{-k(n-1)} \frac{\lambda^n}{n!} e^{-\lambda},$$

where

$$\lambda = q\, 5e^{-s} + (1-q)5e^{-1.2s};$$

and (*C*,*D*) the proportion of males that mate with a female that are efficient harassers, computed as $a/(a+b)$, where

$$a = q\, w_0\, e^{-\lambda} + \sum_{n=1}^{\infty} e^{-k(n-1)} \frac{\lambda^n}{n!} e^{-\lambda} \frac{q\, 5e^{-s}}{q\, 5e^{-s} + (1-q)5e^{-1.2s}},$$

and

$$b = (1-q) w_0\, e^{-\lambda} + \sum_{n=1}^{\infty} e^{-k(n-1)} \frac{\lambda^n}{n!} e^{-\lambda} \frac{(1-q)\, 5e^{-1.2s}}{q\, 5e^{-s} + (1-q)5e^{-1.2s}}.$$

Note that $e^{-\lambda}$ is the probability that the female does not mate in the den and that the speed that maximizes direct benefits can be either lower (*A*,*C*) or higher (*B*,*D*) than the one that is best for finding an efficient male to sire the offspring. The difference is, however, slight. The consequences of this discrepancy are minor for selection acting on males (see text).

techniques to analyze coevolution between resistance and male mating effort, and whether equilibria depends on genetic covariance between female and male traits (e.g., Kokko 2005). Here, to make a conceptual point, we simply assume that efficiency is heritable, so that indirect selection favors mating with efficient harassers to increase sons' mating success.

The fitness of sons is an increasing function of the proportion of mates who are efficient harassers. This proportion depends on female speed in a nonlinear way (Fig. 2C,D). Consider the extremes: Very slow females gain offspring sired by the two male types according to the ratio $5q$:$4(1-q)$ (efficient:inefficient harassers). Very fast females escape the den without mating, and the ratio is q:$1-q$ when mating outside the den. Intermediate speeds are the best for screening purposes. At a relatively high speed, females mate in the den, but most can still escape the mating attempts of inefficient harassers.

These nonlinearities per se are less interesting than realizing that the female speed s that maximizes genetic benefits can be faster or slower than the speed that maximizes direct fitness (Fig. 2A vs. 2C, and 2B vs. 2D). Given how little is known about paternity and fitness outside the den (Shine et al. 2005), nor about other important parameters such as heritabilities and antagonistic (or not) genetic effects on sons' versus daughters' fitness, we do not want to make statements about whether these differences produce a significant shift in female speeds compared with a scenario involving maximizing direct fitness. The point we want to make here is far simpler: It is inappropriate to assume that choosier females will move more slowly (so that faster speeds are automatically indicative of maximization of direct fitness) simply because models of mate choice traditionally use a framework in which sampling more males increases the eventual mate's quality either explicitly (Janetos 1980; Real 1990; Johnstone 1997) or implicitly (i.e., stronger preferences are assumed to be costlier [e.g., Pomiankowski et al. 1991]). In reality, choosiness for genetic benefits can require that more time be spent with males (e.g., when actively sampling displaying males; Byers and Waits 2006) but, as our model shows, it can equally be associated with a reduction in the time spent with males relative to that which minimizes costs. The lesson for empiricists is that all models make assumptions about an organism's natural history. If the biology of a species differs from these assumptions, then generic concepts such as choosiness have to be interpreted carefully.

In the garter snake scenario above, we simply assumed that the genetic trait of interest is the same male trait that is imposing costs on females. In reality the situation can be far more complicated. For example, what if females seek genetic benefits that are uncorrelated with a male's ability to acquire mates? As an illustrative example, female Chinook salmon are more aggressive toward major histocompatibility complex (MHC)-similar males (potentially indicating choice for MHC dissimilarity), but males appear to be able to overcome this preference (Garner et al. 2010). Intriguingly, this study provides evidence that females are better able to control the decision to mate when the sex ratio becomes more female-biased, as offspring MHC diversity was found to increase under such conditions.

Are There True Differences between Models? We Can Think of an Important One

It is often a challenge to determine exactly what females will do if there has been selection for genetic benefits. In the model above there is a sexual asymmetry, however, because selection on male behavior is largely independent of whether these benefits modify female behavior. Being efficient at harassing is strongly selected for in all cases other than when females move at extremely high speed s (and this is only because we arbitrarily assumed that harassment efficiency has no effect outside the den).

Although we have primarily argued for the need to consider sexual selection in the light of sexual conflict, the above sexual asymmetry highlights a more relevant distinction from "traditional" female choice scenarios than the (in reality near identical) degree to which different models involve sexual conflict. In the gar-

ter snakes, selection on male behavior shifts only relatively slightly with changes in the magnitude of female escape effort (*s*). In contrast, in classic female preference models it is difficult to explain the evolution of male traits without considering the nuances of female behavior and the selective forces that act on them. In the former case, female cost-minimization ("resist most matings") permits strong selection on males, whereas in the traditional models, the matter is somewhat less clear. Although models often assume that mating is random if females lack preferences, in reality, scenarios in which females lack costly preferences might still generate nonrandom mating. Males can still be selected to succeed in scramble competition or bear other traits that increase their mate encounter rate ("passive attraction" models [Wiley and Poston 1996]).

CONCLUDING REMARKS: WHAT HAPPENS TO POPULATIONS?

We have argued that there is a sense in which one sex can "win" a conflict. We can ask which sex carries a larger lag load (relative to a sensibly chosen hypothetical alternative state, such as "which sex has greater ability to decide on whether a mating occurs" or "which sex provides parental care"). Understanding such sexual asymmetries is important because females tend to drive demography. Simply put, a population consisting of a majority of males is expected to yield fewer offspring than a population consisting of mostly females (Rankin and Kokko 2007). If females have a high lag load (females "lose"), population fitness will tend to suffer more than when males have a high lag load.

An intriguing example is provided by the cichlid fish *Lamprologus callipterus*, in which breeding sites in empty snail shells are a limited resource (Maan and Taborsky 2008). Males can recognize that they have not spawned with a female and take over her shell so that she loses her current reproductive attempt. The expelled female is typically not yet ready to spawn again and must find another empty shell. Sexual conflict is clear (an individual of sex A would have higher fitness if it could somehow prevent its site from being stolen by individuals of sex B). Males take over nests from females, but not the reverse, indicating a greater female than male lag load. The population-level consequence is that many nests fail. The population would conceivably be more productive if females "won" the conflict.

The most fundamental detrimental population-level consequence of sexual conflict is, of course, the twofold cost of sex. The evolution of anisogamy (Parker et al. 1972; Parker 2014) leads to the great majority of resources used for offspring production only being channeled through females (hence, the expected halving of population growth in sexual populations compared with equivalent asexual counterparts [Lehtonen et al. 2012]). If males always contributed all their energy to improving offspring number or survival and none to the zero-sum game of outcompeting other males, population growth would theoretically double. This statement is, however, accompanied by several caveats. If there is biparental care the cost is less than twofold as males are then also investing into offspring. Even here, however, sexual conflict persists: Two caring parents do not necessarily raise twice as many offspring as a single parent, especially as egg production is still a female-only task. For example, in a data set of 980 bird species, removal of male care led to a 20%, rather than 50%, reduction in female productivity (Sibly et al. 2012). Conversely, if sexual conflict not only results in males failing to provide care but additionally selects for traits that reduce the ability of females to produce offspring, then the costs of sex can be more than twofold (Lehtonen et al. 2012). Population collapse is even theoretically possible (Le Galliard et al. 2005; Rankin et al. 2011).

Short-term demography is, of course, not the final word on the topic of population fitness. We need to consider long-term processes. There are few, if any, species with truly random pair formation and lifelong monogamy to look at the evolutionary consequences of the permanent removal of sexual conflict. We should, however, remind ourselves that there is another way to reproduce that achieves the same end: Asexuality removes both sexual conflict and

sexual selection. It is difficult to reconcile the view that sex, with all the attendant conflict, is ultimately harmful for population fitness, with evidence that asexuality tends not to persist over evolutionary time (Neiman et al. 2005; but see Janko 2014). This could be interpreted as support for the view that sexual selection is ultimately "good" for populations (e.g., Sharp and Agrawal 2013). The difficulty, of course, is that comparisons in which "all else is equal" are a major challenge. Asexual species may retain maladaptive vestigial traits that relate to their previous sexual life cycles (Bengtsson 2009). In addition, asexuality removes not only conflict but also genetic recombination (Neher et al. 2010; Hartfield and Keightley 2012). The costs and benefits of sex and the costs of sexual conflict are measured on different timescales; how to reconcile them is a fascinating topic that deserves greater attention.

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The Relationship between Sexual Selection and Sexual Conflict

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